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An Investigation into Blocking of Filial Imprinting in the Chick During Exposure to a Compound Stimulus

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The occurrence of "blocking" was investigated in jungle fowl chicks (*Gallus gallus spadiceus* B.) in an imprinting situation. In Experiment 1, chicks were simultaneously exposed to two stationary coloured cylinders, either two red cylinders (Group RR), a yellow and a red cylinder (YR), or two yellow cylinders (YY). After six days of exposure, the cylinders were removed from the cages and replaced by a yellow and a blue cylinder (i.e. YB) for each chick. This second phase of the experiment lasted for seven days. When the blue cylinder was presented alone during tests at different stages in Phase 2, the RR birds spent significantly more time with this cylinder and emitted fewer shrill calls than the chicks in the YR and YY groups. In Experiment 2, RR and YY birds were reared as in Experiment 1, except that in the second phase of the experiment they were exposed to a blue cylinder only. In this experiment the development of an attachment to the novel blue cylinder proceeded similarly in the RR and YY birds. In Experiment 3, it was found that chicks that were reared with a yellow and a red cylinder preferred the latter stimulus. Thus, although in the first phase of Experiment 1 the RR birds had been exposed to a more attractive stimulus, in tests during the second phase they spent more time with a novel stimulus (B) than the YY birds. These results are consistent with the suggestion that imprinting to a novel stimulus is "blocked" to some extent when that stimulus is presented in compound with another stimulus to which the animal has previously been exposed.

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It has been reported that young precocial birds can rapidly learn the characteristics of the first conspicuous object to which they were exposed and form an attachment with it (see Bolhuis, de Vos, & Kruijt, this issue, for a review). This phenomenon was termed *Prägung* or "imprinting" (Lorenz, 1935, 1937). Many authors have suggested that imprinting is a unique learning process, one of its characteristics being that it is not dependent upon external reinforcement, such as food or warmth (cf. Bateson, 1966, and Sluckin, 1972, for reviews). Sluckin and Salzen (1961) and Sluckin (1972), when describing imprinting as a form of "perceptual learning" or "exposure learning", also stressed the absence of a need for external reinforcement in the process, in contrast to conditioning. In their view, the young animal becomes imprinted on a particular conspicuous object solely as a result of being exposed to it. Afterwards, it will respond filially to this object and avoid novel objects, a process that Jaynes (1958) has called "emergent discrimination".

The absence of a need for reinforcement is not universally accepted. Several authors have proposed an interpretation of filial imprinting as a form of associative learning, the theory developed by Hoffman and co-workers being the most explicit example (Hoffman, Ratner, & Eiserer, 1972; Hoffman & Ratner, 1973; Hoffman, 1978; Hoffman & Segal, 1983). When interpreting the process as a form of associative learning, a problem arises in identifying the elements of the association.

Dickinson (1980) has described associative learning as a process through which animals discover the causal nature of relationships between certain events. When a certain, initially neutral event (E1), is paired with a motivationally significant event (E2), an animal that is exposed to these pairings will associate these two events. Several factors influence the formation of such an association. One of these is degree of correlation between E1 and E2. The stronger the correlation between the occurrence of E1 and E2 (i.e. the higher the predictive value of E1 for E2), the stronger will the association be. Furthermore, learning proceeds faster with some E1's than with others. In that case, the former E1s are said to be more salient. If several E1s are positively correlated with a particular E2, the amount of association received by each of these E1s depends on whether they are presented to the animal separately or compounded. In the latter case there is competition for association, whereas in the former case there is not. There are two important instances of competition between E1s for association—namely, "overshadowing" (Pavlov, 1927) and "blocking" (Kamin, 1969). Overshadowing occurs when several E1s are always paired with E2 in compound with each other and thus are equally well correlated with E2. An E1 that is part of such a compound stimulus will become less strongly associated with E2 than when it is presented alone. Blocking also occurs when E1s are compounded, but now pairing of the compound stimulus (E1A/E1B) with E2 is preceded by

pairing of one part of the compound stimulus (E1A) with E2. In this case the association between E1B and E2 will be less strong than when there is no pre-exposure to E1A. It is even possible that E1B will not become associated with E2.

According to the theory of Hoffman et al., movement of a conspicuous object provides E2. Other studies have shown, however, that chicks can become imprinted to their static environment (Sluckin & Salzen, 1961; Bateson, 1964) and to stationary objects (Salzen, 1969; Eiserer, 1980). It is conceivable that exposure to a conspicuous stimulus (E1), whether this is moving or not, automatically leads to a "motivationally significant event" (E2). Assuming that such an E2 occurs at presentation of an imprinting object, certain predictions can be made, for instance as regards blocking and overshadowing in an imprinting situation (see Bolhuis, De Vos, & Kruijt, this issue, for further discussion). The present experiments were performed to investigate this matter.

EXPERIMENT 1

In this experiment, chicks were exposed to a compound stimulus after they had been exposed to (1) a different stimulus, (2) one of the elements of the compound and another stimulus, or (3) one of the elements of the compound. The experiment was performed to investigate whether, in chicks that had prior experience with one of the elements of the compound stimulus, development of attachment to the novel element would be blocked.

Methods

Subjects. Fifty-two jungle fowl chicks (*Gallus gallus spadiceus* B.), from five different batches of eggs obtained from the laboratory breeding colony were used. The birds were hatched in an incubator at 37.7°C. Within 8 to 18 h of hatching they were transferred to individual wooden cages (50 × 50 × 50 cm), painted dark green, with a wire-mesh front, facing a blank wall at a distance of 1 m. In each cage there was a 40-W white light bulb (Philips Softone) suspended from the top of the cage, which kept the cage at a temperature of approximately 30°C. Food was available *ad libitum* on the floor in the middle of the cage. Water was provided from a bottle at the front of the cage.

Procedure. During the first six days of life, all chicks were exposed to two coloured wooden cylinders (13 cm high, diameter 4.8 cm) placed in the middle of each of the two back quadrants of the cage and fixed to the floor by means of a screw and a copper tube (diameter 1.2 cm), such that the base of the cylinder was 1.5 cm above floor level. The tops of the cylinders were

TABLE 1
Design of Experiment 1: Colour of the Cylinders to which the
Chicks Were Exposed during Phase 1 and Phase 2

<i>Group</i>	<i>n</i>	<i>Phase 1</i>	<i>Phase 2</i>
RR	16	Red/Red	Yellow/Blue
YR	16	Yellow/Red	Yellow/Blue
YY	20	Yellow/Yellow	Yellow/Blue

pointed. The chicks were divided into three groups (see Table 1), which were exposed to two red cylinders (RR), or one yellow and one red cylinder (YR), or two yellow cylinders (YY), respectively, during the first phase of the experiment. On Day 7, the cylinders were removed from the cages and replaced by one yellow and one blue cylinder (YB) for each chick. The second phase of the experiment lasted from Day 7 until Day 14.

During the second phase of the experiment, a number of tests was performed in a different experimental room. The first test was performed on Day 7, before the stimuli were exchanged. Four further tests were performed on Days 8, 9, 10, and 14. At the beginning of a test, the chick was placed into a cage, similar to the one in which it had been reared. Two petri dishes with water were placed in the front of the cage, and food was on the floor in the middle of the cage. In the cage were a blue and a yellow cylinder, placed on 1.5-cm pedestals, similar to those in the chick's homepage but not fixed to the floor of the cage. By means of overhead wires attached to the top of the two cylinders, they could be lowered and raised through tubes in the top of the test cage, out of sight of the animal. First the animal was exposed for 1 min to the yellow and the blue cylinder, each placed in the middle of one of the two back quadrants of the cage. Subsequently, the animal was given a series of 1-min periods of exposure to either the empty cage (E), the yellow cylinder (Y), the blue cylinder (B), or to the two cylinders simultaneously (YB), according to one of the following two schedules:

- a. E-Y(1)-E-YB(1)-E-B(1)-E-YB(2)-E-Y(2)-E-YB(3)-E-B(2)-E-YB(4)-E
- b. E-B(1)-E-YB(1)-E-Y(1)-E-YB(2)-E-B(2)-E-YB(3)-E-Y(2)-E-YB(4)-E

For each of the three experimental groups, half of the chicks received Schedule a and the other half Schedule b. Thus, in a testing session a chick was exposed to the blue cylinder twice, to the yellow cylinder twice, and to both cylinders simultaneously for four periods of 1 min. During the test the position of the chick in the cage was registered every 5 sec, as well as the

number of shrill calls (cf. Hogan & Abel, 1971; Kruijt, 1985) emitted by the chick during each of the periods of exposure. At the end of each test the chick was returned to its home cage.

The percentage of time spent in quadrants with a cylinder was analysed for each group of chicks on a per day basis, as well as the number of shrill calls in the presence of a cylinder, relative to the number of calls in the empty test cage ("calling ratio"). The calling ratio was calculated according to the following formula:

$$\frac{C}{C+E}$$

where C = calls per min when exposed to the cylinder, and E = calls per min when in the empty test cage. A calling ratio greater than 0.50 means that the chicks called at a higher frequency when exposed to the cylinder than in the empty test cage. A calling ratio less than 0.50 means that exposure to the cylinder had a suppressing effect on shrill calling.

Statistical Analysis. The results were analysed by means of a two-factor analysis of variance (ANOVA) with repeated measures (Winer, 1971), with factors Test (Day 8, 9, 10, or 14) and Group (RR, YR, or YY).

Results

Test Scores on Day 7. During the test on Day 7, the chicks were exposed to the blue cylinder and to the testing apparatus for the first time. During this test, the chicks in all three groups spent little time in quadrants with a cylinder. ANOVA performed on the results for time spent with the blue cylinder when this was presented alone on Day 7 revealed no significant effect of Group [$F < 1$; mean percentage of time spent with the blue cylinder (\pm s.e.m.): RR, 1.8 (\pm 6.3): YR, 2.1 (\pm 7.3): YY, 0.2 (\pm 0.9)]. However, there was a significant effect of Group in respect to time spent with the yellow cylinder when this was presented alone on Day 7, $F(2, 49) = 7.69$, $p < 0.01$, the effect being due to the YY birds, which spent more time with the yellow cylinder than the birds in the other two groups [mean percentage of time spent with the yellow cylinder (\pm s.e.m.): RR, 0.3 (\pm 0.3): YR, 3.4 (\pm 2.3): YY, 24.0 (\pm 6.9)].

On Day 7, the blue and the yellow cylinder had no suppressing effect on shrill calling of chicks in any of the groups. On the contrary, when the chicks were exposed to a cylinder on Day 7, they mostly called at a higher frequency than in the empty cage (calling ratios > 0.50). ANOVA performed on the results for calling ratio when the blue cylinder was presented alone on Day 7 revealed no significant effect of Group [$F < 1$; mean calling ratio (\pm s.e.m.): RR, 0.55 (\pm 0.03): YR, 0.60 (\pm 0.04): YY, 0.57 (\pm 0.03)]. There was also no

significant effect of Group for calling ratio on Day 7, when the yellow cylinder was presented alone [$F(2, 49) = 1.03$, $p > 0.3$: mean calling ratio (\pm s.e.m.): RR, 0.54 (± 0.03): YR, 0.54 (± 0.03): YY, 0.47 (± 0.05)].

The chicks behaved quite differently during the tests on Days 8 to 14 (see below), when they had prior experience with the testing apparatus and had been exposed to the yellow and the blue cylinder in their home cage for one or more days. There are good reasons to believe that on Day 7, the absence of experience with the testing apparatus and, in particular, the absence of experience with the blue cylinder influenced the test results in such a way that differences between groups and tests in respect to attachment of chicks to the blue and yellow cylinder were obscured (see Results section, Experiment 3).

Time Spent with Cylinders on Days 8 to 14. The mean percentage of time spent in the quadrant with the blue cylinder when this was presented alone is shown in Figure 1A for all three groups. ANOVA performed on results of the tests on Days 8 to 14 revealed significant effects of Group, $F(2, 49) = 3.15$, $p = 0.05$, and Test, $F(3, 147) = 29.31$, $p < 0.001$, but no significant interaction between these two factors [$F(3, 147) = 1.40$, $p > 0.2$]. Thus, there was a difference between the groups in time spent with the blue cylinder, whilst the chicks in all the groups spent increasingly more time with this stimulus in the course of the second phase of the experiment. RR birds spent most time with the blue cylinder and YY birds the least.

Figure 1B shows the mean percentage of time spent in the quadrant with the yellow cylinder when this was presented alone. ANOVA performed on the results of Days 8 to 14 revealed a significant effect of Test $F(3, 147) = 15.12$, $p < 0.001$, but not of Group [$F(2, 49) = 2.75$, $p > 0.07$]. Thus, during the tests on Days 8 to 14 there were significant differences between the groups in time spent with the blue cylinder (Figure 1A), but not in time spent with the yellow cylinder (Figure 1B).

The mean percentage of time spent in the quadrant with the blue and yellow cylinder, respectively, when these cylinders were presented simultaneously, is shown in Figure 2. ANOVA performed on results of the tests on Days 8 to 14 revealed, both for time spent with the blue cylinder and for time spent with the yellow cylinder, a significant effect of Test, blue cylinder: $F(3, 147) = 9.83$, $p < 0.001$, yellow cylinder: $F(3, 147) = 4.94$, $p < 0.01$, but not of Group [blue cylinder: $F(2, 49) = 2.06$, $p > 0.1$, yellow cylinder: $F(2, 49) = 1.92$, $p > 0.1$]. Thus, during the tests on Days 8 to 14 there were overall no statistically significant differences between the groups in time spent with the blue and with the yellow cylinders when these were presented simultaneously. However, the observed differences were in the same direction as those observed when the cylinders were presented alone. Time spent with the blue cylinder is of special interest here. As can be seen in Figure 2A, RR chicks spent on average most time with this cylinder, and YY chicks the least.

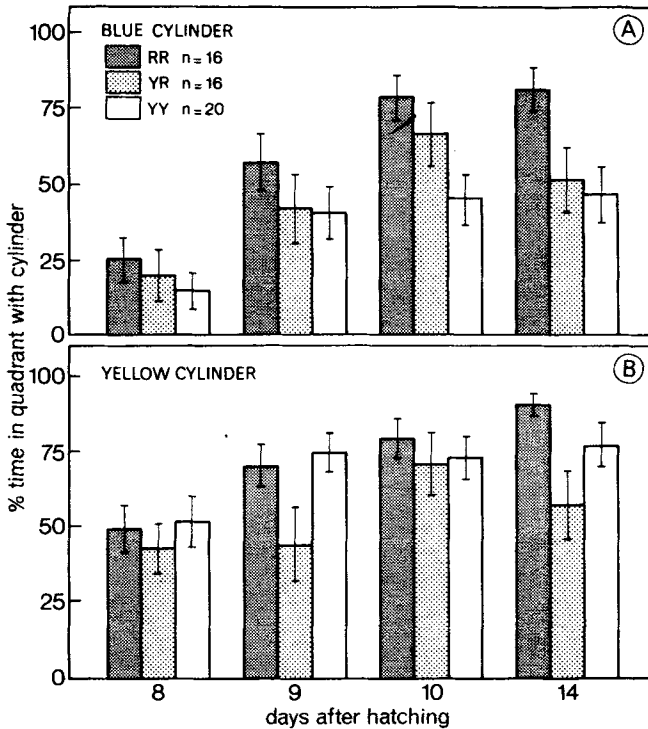


FIG. 1. Mean percentage of time (\pm s.e.m.) spent in the quadrant of the test cage with (A) the blue cylinder and (B) the yellow cylinder when these cylinders were presented alone during tests in Experiment 1.

ANOVA performed on the results for Day 14 revealed that on this day groups differed significantly in mean percentage of time spent with the blue cylinder when this was presented simultaneously with the yellow cylinder, $F(2, 49) = 3.43$, $p < 0.05$.

Calling Frequency on Days 8 to 14. Table 2 shows the mean levels of calling in the empty cage during the tests on Days 8 to 14. There was no significant effect of Group [$F(2, 49) = 0.61$, $p > 0.5$], nor of Test [$F(3, 147) = 2.03$, $p > 0.1$]. Thus, the mean frequency of calling in the absence of cylinders was similar for the three groups and remained at the same level during the four testing days.

Figure 3A shows the mean calling ratio when the blue cylinder was presented alone during the tests. ANOVA performed on the results of Days 8 to 14 showed a significant effect of Test, $F(3, 147) = 10.23$, $p < 0.001$, but not of Group [$F(2, 49) = 2.50$, $p = 0.09$]. As can be seen in Figure 3A, the level of

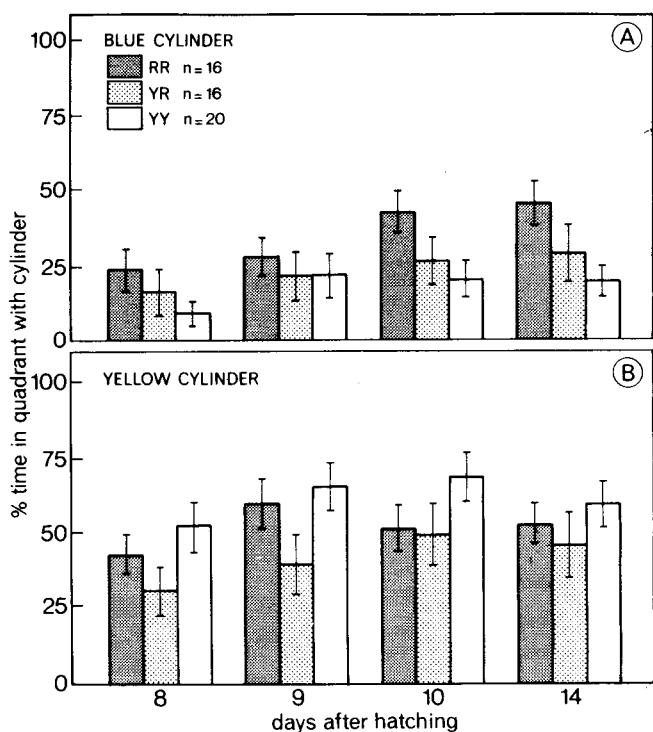


FIG. 2. Mean percentage of time (\pm s.e.m.) spent in the quadrant of the test cage with (A) the blue cylinder and (B) the yellow cylinder when these cylinders were presented simultaneously during tests in Experiment 1.

TABLE 2
Mean Number of Shrill Calls per Minute in the Empty Cage during Tests in Experiment 1

Group	Day							
	8		9		10		14	
	Mean	s.e.m.	Mean	s.e.m.	Mean	s.e.m.	Mean	s.e.m.
RR	62.9	7.7	75.0	7.0	81.1	6.6	82.8	5.4
YR	71.5	6.7	71.6	7.9	68.7	8.0	74.6	5.4
YY	77.2	6.3	84.4	5.1	77.9	6.3	79.0	4.2

calling in the presence of the blue cylinder was relatively low throughout Days 8 to 14 in the RR group. The calling level in the other two groups was higher on Day 8 but decreased until, on Day 14, there was no difference between the three groups. The effect of Group was significant on Day 8, $F(2, 49) = 4.07$, $p < 0.05$, but not on Day 14 [$F(2, 49) = 0.17$, $p > 0.8$]. ANOVA performed on the results of Days 8 to 10 revealed that over this period there was a significant effect of group, $F(2, 49) = 3.74$, $p < 0.05$, and of test, $F(2, 98) = 9.30$, $p < 0.001$, but no significant interaction between these two factors [$F(2, 98) = 0.77$, $p > 0.5$].

The mean calling ratio when the yellow cylinder was presented alone is shown in Figure 3B. ANOVA performed on the results of Days 8 to 14 revealed a significant effect of Group, $F(2, 49) = 4.17$, $p < 0.05$, and of Test, $F(3, 147) = 13.04$, $p < 0.001$, but no significant interaction between these two factors [$F(3, 147) = 1.40$, $p > 0.2$]. Figure 3B indicates that the effect of Group is mainly due to the high calling frequency of chicks in the YR group.

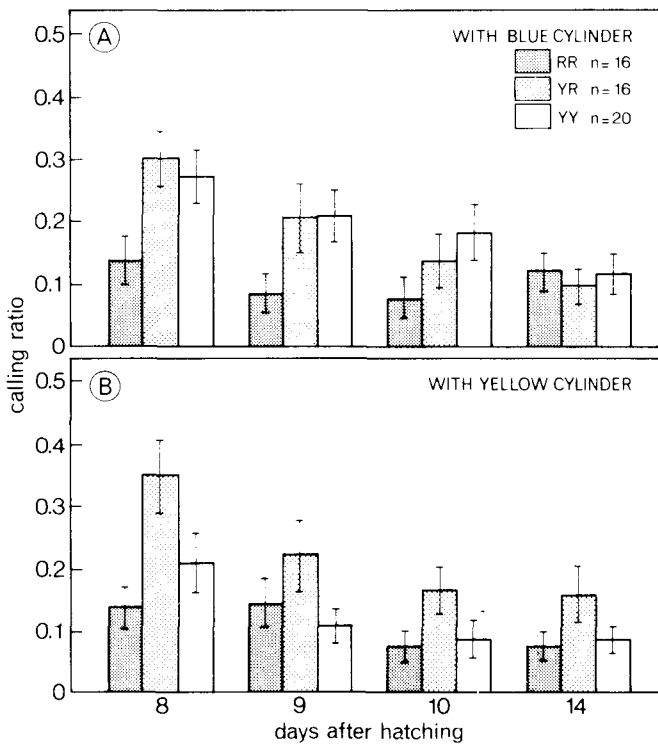


FIG. 3. Mean calling ratio (\pm s.e.m.) for periods in which (A) the blue cylinder, and (B) the yellow cylinder were presented alone during tests in Experiment 1.

Thus, calling levels were relatively low in RR birds when exposed to the blue cylinder (Figure 3A), and in RR and YY birds when exposed to the yellow cylinder (Figure 3B). Calling levels were relatively high in YR and YY birds when exposed to the blue cylinder on Days 8 to 10 (Figure 3A), and in YR birds when exposed to the yellow cylinder (Figure 3B). In interpreting these data, it must be kept in mind that during the tests on Days 8 to 14 exposure to either the blue or the yellow cylinder had a profound suppressing effect on shrill calling of the chicks in all three groups (calling ratios < 0.50).

Discussion

When socially isolated chicks are raised with a cylinder, they spend considerable amounts of time close to the cylinder. Attachment to the cylinder can be experimentally demonstrated by removing the cylinder, or by exchanging it for another with a different colour. In the absence of the familiar cylinder, eating, drinking, and comfort behaviour, such as preening, disappear and shrill calling becomes the predominant activity (Kruijt, 1985). In the present experiment, time spent close to cylinders and frequency of shrill calling when exposed to cylinders were used to measure attachment of chicks in three groups (RR, YR, and YY) to the elements of a compound stimulus (the blue and the yellow cylinders). The results on time spent with the cylinders, as well as those on calling frequency when exposed to a cylinder, indicate that development of attachment to the novel blue cylinder in the second phase of the experiment did not proceed equally in chicks of the three groups. The data about calling frequency when exposed to the blue cylinder suggest that RR chicks became most rapidly attached to the blue cylinder (Figure 3A), and the data about time spent with the blue cylinder suggest that RR chicks eventually became strongest attached to this cylinder (Figures 1A and 2A). This issue will be further discussed in the General Discussion section.

EXPERIMENT 2

The differences between the groups in Experiment 1 with respect to the development of an attachment to the novel blue cylinder in Phase 2, may be the result of blocking by the familiar yellow cylinder in Phase 2 in Groups YR and YY. However, it may also be an effect of different treatments of the groups in Phase 1. That is, it is conceivable that when chicks are exposed only to a blue cylinder in the second phase of the experiment, rather than to a compound of a blue and a yellow cylinder, RR chicks would also become more rapidly attached to the blue cylinder than YY birds. The present experiment was performed to test this possibility.

Methods

Subjects. Forty-seven jungle fowl chicks were used, from four different batches of eggs. The chicks were hatched and reared as in Experiment 1.

Procedure. The chicks were divided into two groups (see Table 3), that were exposed to two red cylinders (RR) or two yellow cylinders (YY), respectively, during the first phase of the experiment. At the beginning of Phase 2, on Day 7, the cylinders were removed from the cages and replaced by a blue cylinder in one of the back quadrants of the cage for each chick. The second phase of the experiment lasted from Day 7 until Day 15.

The chicks were tested in a cage similar to that in Experiment 1, on Days 7 (before the cylinders were exchanged), 8, 9, 10, and 15. At the beginning of a test the animal was placed in the test cage with a blue cylinder for 1 min. Subsequently the animal received a series of 1-min periods of exposure to either the empty cage (E) or the blue cylinder (B), according to the following schedule:

E-B(1)-E-B(2)-E-B(3)-E

As in Experiment 1, the time spent in the different quadrants of the test cage and the number of shrill calls in each of the 1-min periods of exposure was measured.

Statistical Analysis. The results were analysed by means of a two-factor analysis of variance with repeated measures, with factors test (Day 8, 9, 10, or 15) and group (RR or YY).

Results

Test Scores on Day 7. The chicks in Experiment 2, like those in Experiment 1, spent little time in the quadrant with the blue cylinder during the test on Day 7, and during that test the blue cylinder had no suppressing

TABLE 3
Design of Experiment 2: Colour of the Cylinders to which the
Chicks Were Exposed during Phase 1 and Phase 2

Group	n	Phase 1	Phase 2
RR	24	Red/Red	Blue
YY	23	Yellow/Yellow	Blue

effect on shrill calling of the chicks. A Student *t*-test performed on the results for time spent with the blue cylinder on Day 7 revealed no significant difference between the two groups [$t(45)=0.32$, $p>0.7$; mean percentage of time spent with the blue cylinder (\pm s.e.m.): RR, $3.1 (\pm 1.2)$; YY, $2.5 (\pm 1.4)$]. A Student *t*-test performed on the results for calling ratio with the blue cylinder on Day 7 also revealed no significant difference between the two groups [$t(45)=0.38$, $p>0.7$; mean calling ratio with the blue cylinder (\pm s.e.m.): RR, $0.56 (\pm 0.03)$; YY, $0.55 (\pm 0.02)$]. Thus, Groups RR and YY were similar in respect to test scores on Day 7.

Time Spent with the Blue Cylinder on Days 8 to 15. The mean percentage of time spent in the quadrant with the blue cylinder is shown in Figure 4 for both groups. ANOVA performed on results of the tests on Days 8 to 15 revealed a significant effect of Test, $F(3, 153)=22.78$, $p<0.001$, but not of Group [$F(1, 45)=0.02$, $p>0.8$]. Thus, the chicks in both groups spent increasingly more time with the blue cylinder in the course of the second phase of the experiment, and time spent with the cylinder was similar for both groups.

Calling Frequency on Days 8 to 15. Table 4 shows the mean level of shrill calling in the empty test cage on Days 8 to 15. ANOVA performed on these results revealed a significant effect of Test, $F(3, 135)=3.12$, $p=0.03$, but not of Group [$F(1, 45)=1.07$, $p=0.3$]. Thus, calling frequency in the absence of the blue cylinder varied between tests but was not significantly different for the two groups. As can be seen in Table 4, there was no systematic increase or decrease in calling frequency in the empty cage in the course of the second phase of the experiment.

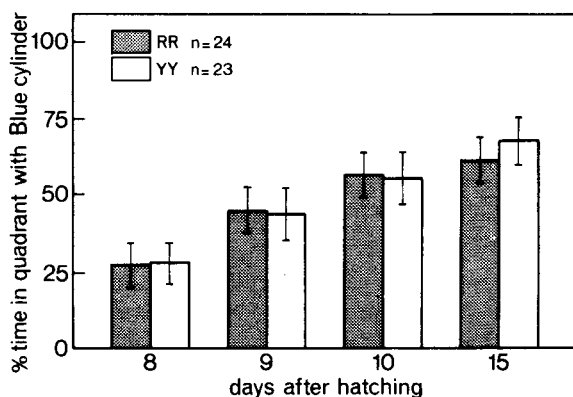


FIG. 4. Mean percentage of time (\pm s.e.m.) spent in the quadrant of the test cage with the blue cylinder when this was presented during tests in Experiment 2.

TABLE 4
Mean Number of Shrill Calls per Minute in the Empty Cage during Tests in Experiment 2

Group	Day							
	8		9		10		15	
	Mean	s.e.m.	Mean	s.e.m.	Mean	s.e.m.	Mean	s.e.m.
RR	78.3	6.9	86.4	7.1	94.0	6.0	83.4	6.1
YY	72.4	6.5	84.6	6.5	75.2	7.1	76.5	6.1

The mean calling ratio when the blue cylinder was presented is shown in Figure 5 for both groups. ANOVA performed on the results of Days 8 to 15 revealed a significant effect of Test, $F(3, 135) = 16.95$, $p < 0.001$, but not of Group [$F(1, 45) = 0.04$, $p > 0.8$]. Thus, calling in the presence of the blue cylinder decreased in the course of the second phase of the experiment, and calling ratio with the blue cylinder was similar for both groups.

Discussion

The results on time spent with the blue cylinder, as well as those on calling frequency when exposed to the blue cylinder, show that (1) chicks in both groups (RR and YY) became attached to the novel blue cylinder, and (2) development of attachment proceeded similarly in both groups of chicks. This implies that the differences observed between the groups in Experiment 1 in the development of an attachment to the novel blue cylinder in Phase 2

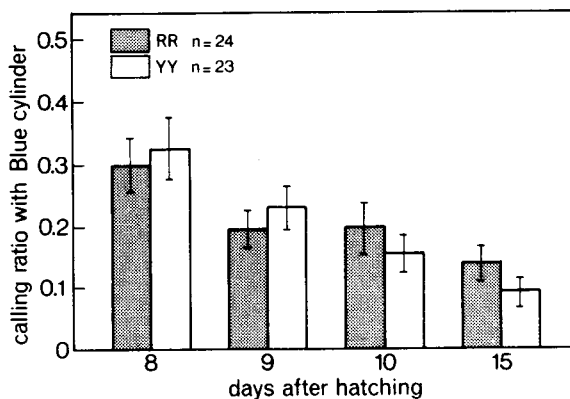


FIG. 5. Mean calling ratio (\pm s.e.m.) for periods in which the blue cylinder was presented during tests in Experiment 2.

are most probably not an effect of different treatments of the groups in Phase 1 of the experiment.

EXPERIMENT 3

Experiments on colour preferences in domestic and jungle fowl chicks have shown that red objects are more attractive to naive chicks than yellow ones, and that they are also more salient imprinting stimuli (Schaefer & Hess, 1959, and unpublished results from our laboratory). The present experiment was performed to see whether in our experimental conditions the red cylinder was also a more salient stimulus than the yellow cylinder.

Methods

Subjects. The subjects were 18 jungle fowl chicks from two different batches of eggs. The chicks were hatched and reared as in Experiment 1.

Procedure. The chicks were exposed to one yellow and one red cylinder during the first 6 days after hatching. In the second phase of the experiment, which lasted from Day 7 until Day 14, the chicks were exposed to the same cylinders as in the first phase. In the second phase the animals received tests with the yellow and red cylinder on Days 7, 8, 9, 10, and 14, according to one of the following schedules:

- a. E-Y(1)-E-YR(1)-E-R(1)-E-YR(2)-E-Y(2)-E-YR(3)-E-R(2)-E-YR(4)-E
- b. E-R(1)-E-YR(1)-E-Y(1)-E-YR(2)-E-R(2)-E-YR(3)-E-Y(2)-E-YR(4)-E

At the beginning of a test the animal was placed in the test cage with a yellow and a red cylinder for 1-min. After that, the birds in one half of the group received a series of 1-min periods of exposure to the stimuli or the empty test cage according to Schedule a and the other half to Schedule b. As in Experiment 1, the time spent in the different quadrants of the test cage and the number of shrill calls in each of the 1-min periods of exposure was measured.

Statistical Analysis. The results were analysed by means of a two-factor analysis of variance with repeated measures on both factors, colour (red cylinder, yellow cylinder, or both cylinders presented) and test (Day 8, 9, 10, or 14).

Results

Test Scores on Day 7. During the test on Day 7, the chicks in Experiment 3 were exposed to the testing apparatus for the first time, but, contrary to the chicks in Experiment 1, they were not exposed to an unfamiliar cylinder. The birds in Experiment 3 and the YR birds in Experiment 1 received exactly the same experience until the beginning of the test on Day 7. Thus, a comparison of testing scores between these two groups is useful to evaluate effects of exposure to the unfamiliar blue cylinder on the scores of the YR birds in Experiment 1 during exposure to the familiar yellow cylinder. Chicks in both groups spent little time in the quadrant with the yellow cylinder when this was presented alone on Day 7, but the mean percentage of time spent with the yellow cylinder was higher for the chicks in Experiment 3 [mean (\pm s.e.m.): Experiment 1 3.4 (\pm 2.3), Experiment 2, 13.2 (\pm 5.9)]. A Student *t*-test revealed that this difference was not statistically significant [$t(32) = 1.55$, $p > 0.2$]. Whereas shrill calling of the YR chicks in Experiment 1 increased when they were exposed to the yellow cylinder alone on Day 7 [mean calling ratio (\pm s.e.m.): 0.54 (\pm 0.03)], exposure to the yellow cylinder on Day 7 suppressed calling of the chicks in Experiment 3 [mean calling ratio (\pm s.e.m.): 0.42 (\pm 0.03)]. A Student *t*-test revealed that this difference was statistically significant, $t(32) = 2.92$, $p < 0.01$. These differences in test scores between the YR chicks in Experiment 1 and the chicks in Experiment 3 indicate that exposure to an unfamiliar cylinder during a test may affect the scores for the familiar cylinder in the same test. This effect may obscure differential attachment of chicks to the cylinders presented in the tests.

When, for the chicks in Experiment 3, test scores on subsequent days were compared, it appeared that the greatest differences were those between Days 7 and 8. This indicates that experience with the test situation influenced the testing scores. This kind of experience accumulated in subsequent tests but was completely absent in the first test on Day 7.

Time Spent with Cylinders on Days 8 to 14. The percentage of time spent in the quadrant with the red or yellow cylinder when these were presented alone is shown in Figure 6A. ANOVA performed on the results of Days 8 to 14 revealed significant effects of Colour, $F(1, 17) = 10.74$, $p < 0.01$, and of Test, $F(3, 51) = 5.25$, $p < 0.01$, and no significant interaction between these two factors [$F(3, 51) = 1.05$, $p > 0.3$]. The percentage of time spent in the quadrant with the red or yellow cylinder when these were presented simultaneously is shown in Figure 6B. ANOVA performed on the results of Days 8 to 14 revealed significant effects of Colour, $F(1, 17) = 21.41$, $p < 0.001$, and of Test, $F(3, 51) = 5.86$, $p < 0.01$, and a significant interaction between these factors, $F(3, 51) = 4.03$, $p < 0.05$. Thus, the chicks spent more time with

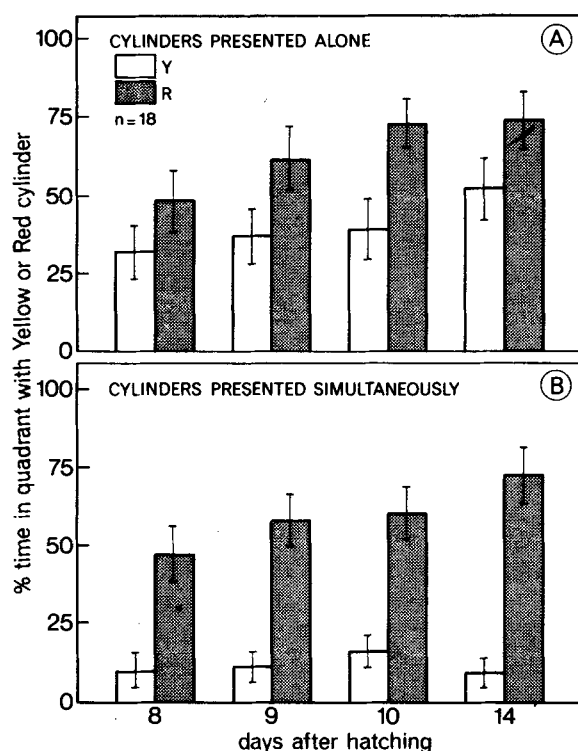


FIG. 6. Mean percentage of time (\pm s.e.m.) spent in the quadrant of the test cage with the yellow or the red cylinder when these cylinders were (A) presented alone or (B) presented simultaneously during tests in Experiment 3.

the red than with the yellow cylinder, and the time they spent with the cylinders increased in the course of the experiment. Results of the simultaneous exposure condition indicate that the preference for the red cylinder increased in the course of the experiment, but the results of the separate exposure condition contain no indications for an increasing preference for the red cylinder.

Calling Frequency on Days 8 to 14. Table 5 shows the mean level of shrill calling in the empty cage on Days 8 to 14. ANOVA did not show a significant effect of Test [$F(3, 51) = 0.47, p > 0.7$]. Thus, as in Experiment 1, the mean frequency of calling in the absence of cylinders remained at the same level during the four testing days.

Figure 7 shows the mean calling ratio for periods in which the yellow cylinder alone, the red cylinder alone, or both cylinders simultaneously were presented during the tests. ANOVA performed on the results of Days 8 to 14

TABLE 5
Mean Number of Shrill Calls per Minute in the Empty Cage during Tests in Experiment 3

Day							
8		9		10		14	
Mean	s.e.m.	Mean	s.e.m.	Mean	s.e.m.	Mean	s.e.m.
88.3	6.7	88.9	6.5	84.6	6.0	84.5	3.7

revealed a significant effect of Colour $F(2, 34) = 32.02$, $p < 0.001$, and of Test $F(3, 51) = 4.80$, $p < 0.01$, and no significant interaction between these two factors [$F(6, 102) = 0.60$, $p > 0.7$]. Thus, the red cylinder had a stronger suppressive effect on shrill calling than the yellow cylinder, and the level of suppression caused by the cylinders increased in the course of the experiment.

Discussion

The results of Experiment 3 show that the chicks became attached to both the red and the yellow cylinder, as appears from the time spent in quadrants with a cylinder and the suppression of shrill calling during exposure to a cylinder. However, the chicks preferred the red cylinder to the yellow cylinder, suggesting that the former is the more salient of the two.

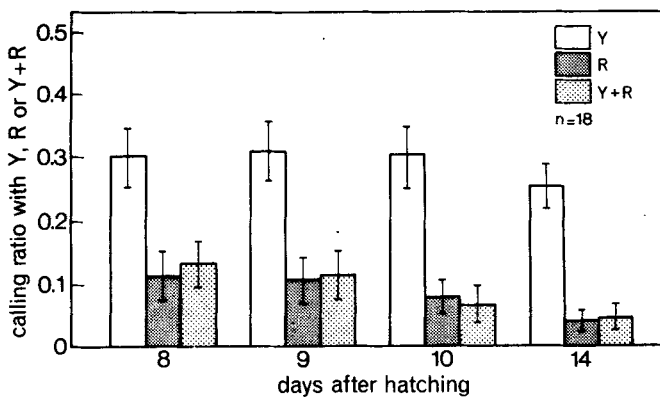


FIG. 7. Mean calling ratio (\pm s.e.m.) for periods in which the yellow cylinder alone, the red cylinder alone, or both cylinders simultaneously were presented during tests in Experiment 3.

GENERAL DISCUSSION

Changes in Test Results over Time

In general, time spent in quadrants with a cylinder increased and frequency of shrill calling when exposed to cylinders decreased in the course of the experiments. There are several possible explanations for this change in testing results over time. First, it might reflect habituation to the testing procedure. In the Results section of Experiment 3, we argued that habituation to the testing apparatus might have been a causal factor underlying the difference in testing results between Days 7 and 8. Habituation might also have played a role in causing the change in testing results from Days 8 to 14/15. An argument against habituation to the testing situation over this period seems to be that the mean frequency of calling in the empty cage remained at the same level over this period. However, it is quite likely that absence of a change over time in calling frequency in the empty cage is the result of a "ceiling effect", the chicks calling at highest sustainable rate in the empty cage during the tests on Days 8 to 14/15. At first sight, a counterargument against this possibility is that the chicks in Experiments 1 and 2, when exposed to a cylinder on Day 7, mostly increased their calling frequency above the level in the empty cage. However, in Experiments 1 and 2, the absolute calling frequency in the empty cage was relatively low on Day 7 compared to Days 8 to 14/15. During exposure to a cylinder on Day 7, the chicks in Experiments 1 and 2 increased their absolute calling frequency to about the level of calling in the empty cage on Days 8 to 14/15. Thus, habituation to the test situation cannot be excluded as a causal factor underlying the change in test results from Days 8 to 14/15.

A comparison of results from Experiments 1 and 3 reveals that habituation cannot be the only factor responsible for the change over time in test results. One argument for this contention is that the change in results is more pronounced in Experiment 1 than in Experiment 3 (e.g. compare Figures 1 and 6A, and 3 and 7). It cannot be excluded that in Experiment 3 learning about the cylinders had ceased at the beginning of the testing period, and that in this experiment habituation to the test situation was the only factor causing a change in results over time. The more pronounced change over time in the results of Experiment 1 indicates that in any case in this experiment attachment of the chicks to the cylinders increased over time.

Attachment to Cylinders at the Beginning of Phase 2

For the interpretation of the results of Experiment 1, it is important to know how strongly chicks in the different groups were attached to their cylinders at

the beginning of Phase 2. We have only indirect information about this for the RR and YY chicks, but for the YR chicks, Experiment 3 provides more direct information. Until the beginning of testing on Day 7, YR chicks in Experiment 1 received exactly the same experience as the chicks in Experiment 3. Thus, YR chicks in Experiment 1 must, at the beginning of testing, have been equally strongly attached to their cylinders as the chicks in Experiment 3. As we have seen, throughout the testing period, the chicks in Experiment 3 appeared to be attached to both the yellow and the red cylinder, but considerably more strongly to the red than to the yellow one. The results of Experiment 3 indicate that the red cylinder is an effective imprinting stimulus. Therefore, there can be little doubt that the RR chicks were strongly attached to this cylinder at the beginning of Phase 2. At that moment, the YY chicks must have been at least as strongly attached to the yellow cylinder as the YR chicks. Most probably, red overshadowed yellow during imprinting of YR chicks in phase 1. This implies that YY chicks were probably more strongly attached to the yellow cylinder than YR chicks. At the beginning of Phase 2, YY chicks may even have been as strongly attached to the yellow cylinder as RR chicks were to the red cylinder.

The results of our experiments contain some concrete evidence that overshadowing occurred in YR chicks in Phase 1, and that YY chicks, at the beginning of Phase 2, were indeed more strongly attached to the yellow cylinder than YR chicks. As discussed in the Results section of Experiment 1, during the test on Day 7, YY chicks spent significantly more time with the yellow cylinder when this was presented alone, than YR chicks. Results of other experiments conducted in our laboratory also indicated that overshadowing occurs when socially isolated chicks are raised in a cage with two different-coloured cylinders.

Differences Between Groups in Learning About the Blue Cylinder

The results of Experiment 1 contain strong evidence that learning about the novel blue cylinder did not proceed at equal speed in all three groups, and that RR chicks learned most rapidly (see Figures 1A and 3A). It is remarkable that on Day 8, only one day after introduction of the blue cylinder, RR chicks when exposed to this cylinder called at about the same level as the chicks in Experiment 3 when these were exposed to the red cylinder, to which, as we have seen, they were strongly attached (see Figures 3A and 7). The data about calling frequency suggest that no further learning occurred in RR chicks after Day 8 or 9 (Figure 3A), but the data about time spent with the blue cylinder (Figure 1A) contradict this and suggest that learning proceeded until Day 10. The data about calling frequency, as well as the data about time spent with the blue cylinder, indicate that learning

proceeded much slower in YR and YY chicks. The data on calling frequency suggest that chicks in the latter groups were still learning at Day 10. The data about time spent with the blue cylinder indicate that the YR and YY chicks eventually became less strongly attached to the blue cylinder than the RR chicks.

An Associative Learning Interpretation

The present results are consistent with an interpretation of filial imprinting as a form of associative learning. In accordance with predictions from animal learning theory, blocking occurred in a filial imprinting situation. Chicks were exposed to a compound of two stimuli (the blue and the yellow cylinder), and those that had been pre-exposed to one of the elements of the compound (the YR and YY chicks) learned less rapidly, and eventually became less strongly attached to the novel stimulus (the blue cylinder) than the chicks that had not previously been exposed to this stimulus but had received exposure to different stimuli (the RR chicks). The results of Experiment 2 support the conclusion that this is due to blocking of filial imprinting in the YR and YY chicks to the novel stimulus, and not simply an after-effect of different treatments of the groups of chicks before exposure to the novel stimulus.

Within an associative learning interpretation of filial imprinting, blocking should occur only if animals have previously become attached to one of the elements of a new compound of stimuli. The formerly established attachment hampers establishment of attachment to the novel element(s) of the compound. As we have seen before, there are good reasons to assume that the YR and YY chicks in Experiment 1 were attached to the yellow cylinder at the beginning of Phase 2 of the experiment. However, the results about reaction to the yellow cylinder on Days 8 to 14 (Figures 1B and 3B) seem to indicate that during the testing phase, RR chicks were at least as strongly, and possibly more strongly, attached to the yellow cylinder as YR and YY chicks. If this were true, animal learning theory would not predict differential learning about the blue cylinder in the YR and YY chicks on the one hand and the RR chicks on the other hand.

In the Results section of Experiment 3, we presented evidence indicating that in YR chicks, the scores for the yellow cylinder, when this was presented alone on Day 7, differed between tests with the yellow and the familiar red cylinder (Experiment 3), and tests with the yellow and the unfamiliar blue cylinder (Experiment 1). In the latter tests chicks called at a higher frequency when exposed to the yellow cylinder alone, and, although this effect was not statistically significant, they spent less time in the quadrant with this cylinder. This effect of exposure to an unfamiliar cylinder tends to obscure differential attachment of chicks in different groups to the yellow cylinder, the YR and

YY chicks being more strongly attached to this cylinder than appears from the scores for the yellow cylinder. Thus, the scores for the yellow cylinder as shown in Figures 1B and 3B are not a strong argument against the conclusion that attachment to the yellow cylinder blocked imprinting on the unfamiliar blue cylinder in the YR and YY chicks. These scores might in fact be interpreted as circumstantial evidence in favour of this conclusion. When it is assumed that YR and YY chicks must have been more strongly attached to the yellow cylinder than RR chicks, the fact that this is not reflected in the test scores for the yellow cylinder indicates that the development of an attachment to the blue cylinder proceeded slower in YR and YY chicks than in RR chicks.

The results of Experiment 1 might be interpreted in terms of blocking, but it is clear that development of an attachment to the novel blue cylinder was not completely blocked in YR and YY chicks. At the end of the experiment, these chicks spent a considerable amount of time with the blue cylinder when this was presented alone (Figure 1A), and exposure to the blue cylinder strongly suppressed their shrill calling (Figure 3A). This result was to be expected for the YR chicks, which, as a result of overshadowing of yellow by red in Phase 1, will have been only partially imprinted on the yellow cylinder at the beginning of Phase 2. More complete blocking would have been expected for the YY chicks. There are several possible explanations for the incompleteness of blocking in this group. One possibility is that imprinting was not yet complete at the end of Phase 1. In this case, animal learning theory does not predict complete blocking in Phase 2. A second possibility is that generalization occurred, the blue cylinder being attractive to the chicks because of its similarity in form to the yellow cylinder. It is also possible that the testing periods in which the chicks were exposed to the blue cylinder alone resulted in "unblocking" of learning about the blue cylinder. The present results do not allow a conclusion about the effectiveness of each of these factors in causing incomplete blocking of imprinting on the blue cylinder in YY chicks.

During the second phase of Experiment 1, chicks may have received differential visual input from the elements of the compound stimulus, depending on their previous experience, and this may have played an important role in causing the blocking of imprinting in the YR and YY groups. That is, chicks that had been exposed to the yellow cylinder in Phase 1 are likely to have formed an attachment to this stimulus. Consequently, in Phase 2 these chicks will preferentially have positioned themselves near the yellow cylinder, and they may have spent more time looking at this cylinder than at the blue one. YR and YY chicks may thus have received differential visual input from the elements of the compound stimulus, and this may have resulted in impaired attachment of these chicks to the blue cylinder, compared to RR chicks. Selective attention is also supposed to play an

important role in conventional associative learning paradigms (e.g. the Mackintosh and Pearce–Hall theories; cf. Pearce, 1987, pp. 151–180), but attentional theories of associative learning refer to attention as the degree of analysis that sensory inputs receive (cf. Glass & Holyoak, 1986, pp. 33–75), and assume that the animal receives equal input from the different stimuli. Thus, although “blocking” has been demonstrated to occur in imprinting as a behavioural phenomenon (which is interesting in itself, both from a causal and a functional point of view), the underlying causal mechanism might not be the same as that which is supposed to underlie blocking in conventional associative learning paradigms. However, in order to examine whether underlying mechanisms are shared between associative learning and imprinting, it is necessary in the first place to establish that phenomena that occur in associative learning (and that have played an important role in the development of learning theories) also occur in imprinting. The issue whether blocking of imprinting is dependent upon selective sampling of information by the animal could be further investigated by experiments in which exposure of chicks to the two stimuli is controlled, e.g. by using a compound of a visual and an auditory stimulus.

Final Conclusions

The present results are consistent with an associative learning interpretation of filial imprinting. They confirm previous observations (e.g. Eiserer, 1980) that chicks can become imprinted on stationary objects, showing that movement of the stimulus is not a necessary E2 for imprinting as has been proposed by Hoffman et al. (1972). The results do not reveal how the conspicuous object can provide an E2 for associative learning to proceed. When it is assumed that presentation of a conspicuous object provides an E2, the present experiments suggest how an associative learning interpretation of imprinting might be tested. The results are consistent with such an interpretation, but further research is required to be able to rule out alternative explanations.

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Etude du blocage de l'empreinte filiale chez le poussin lors de l'exposition à un stimulus composite

Le phénomène de blocage a été étudié chez le Coq de Java (*Gallus gallus spadiceus* B.) en situation d'empreinte. Dans l'expérience 1, on présente simultanément aux poussins deux cylindres colorés, fixes: soit deux cylindres rouges (groupe RR), soit un jaune et un rouge (YR), soit 2 jaunes (YY). Les cylindres sont retirés des cages au bout de six jours et remplacés par un cylindre jaune et un cylindre bleu (YB) pour chaque sujet. Cette deuxième phase dure sept jours. Au cours des tests, quand le cylindre bleu est présenté seul, à différentes étapes de la phase 2, les poussins RR passent significativement plus de temps avec ce cylindre et émettent moins d'appels

stridents que les sujets des groupes YR et YY. Dans l'expérience 2, les sujets RR et YY sont soumis aux mêmes conditions que dans l'expérience 1, à la différence que dans la seconde phase, on ne leur présente qu'un cylindre bleu. Dans cette expérience, le développement de l'attachement au cylindre bleu, nouveau, se réalise de la même manière que chez les groupes RR et YY. Dans l'expérience 3, il est montré que les sujets élevés avec un cylindre jaune et un cylindre rouge préfèrent ce dernier stimulus. Il apparaît donc que, bien qu'ayant été exposés à un stimulus plus attractif lors de la première phase, les sujets du groupe RR passent, lors des tests, plus de temps avec un nouveau stimulus (B) que les sujets du groupe YY. Ces résultats sont en accord avec l'hypothèse selon laquelle l'empreinte à un stimulus nouveau est bloquée, dans une certaine mesure, quand ce stimulus est présenté en association avec un autre stimulus auquel le sujet a été préalablement exposé.

Un estudio de bloqueo de la impronta filial en el pollo durante la exposición a un estímulo compuesto

La ocurrencia de bloqueo ("blocking") durante el establecimiento de impronta filial fue investigada en pollos de *Gallus gallus spadiceus* B. En el primer experimento los pollos fueron expuestos simultáneamente a dos cilindros coloreados estacionarios, siendo ambos rojos (grupo RR), uno amarillo y otro rojo (grupo YR) o ambos amarillos (grupo YY). Luego de seis días de exposición los cilindros fueron removidos de las cajas y reemplazados por un cilindro azul y otro amarillo (YB) en todos los casos. Esta segunda fase del experimento duró siete días. Cuando el cilindro azul fue presentado aisladamente en pruebas intercaladas en la segunda fase las aves RR pasaron significativamente más tiempo con este cilindro y emitieron menos llamados de peligro que las aves de los grupos YR y YY. En el experimento 2, las aves RR y YY fueron criadas en las mismas condiciones del primer experimento salvo que, en la segunda fase, fueron expuestas sólo a un cilindro azul. En este experimento el desarrollo de una atracción por el nuevo cilindro azul fue similar en ambos grupos RR y YY. En el experimento 3 se encontró que los pollos criados con un cilindro amarillo y uno rojo mostraron preferencia por el último. Aunque en la primer fase del experimento 1 las aves RR fueron expuestas a un estímulo más atractivo, en las pruebas de la segunda etapa pasaron más tiempo con el estímulo nuevo (B) que las aves YY. Estos resultados son consistentes con la sugerencia de que la impronta a un estímulo nuevo es "bloqueada" en cierta extensión cuando ese estímulo se presenta en composición con otro estímulo al cual el animal ha sido ya expuesto.